



The Physiological and Morphological Effects of Seaweed Application On Tobacco Seedling Characters and Quality (*Nicotiana tabacum* L.) Plants Under Salt Stress

İbrahim Halil Şındak¹ · Halit Karagöz¹ · Mahmut Tepecik² · Sıdıka Ekren¹

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Abstract

This study aimed to evaluate the effects of seaweed extract application on the morphological, physiological, and nutrient characteristics of tobacco plants (*Nicotiana tabacum* L.) grown under salt stress conditions. Plant growth, biomass production, leaf morphology, chlorophyll content, quality traits, and macro nutrient contents were assessed. The evaluated parameters included plant height, root and stem fresh and dry weights, leaf length, width, area, number of leaves, chlorophyll content, nicotine and ash ratios, and the concentrations of nitrogen, phosphorus, potassium, calcium, and magnesium. Salt stress markedly reduced plant growth and nutrient accumulation in tobacco plants. In contrast, seaweed extract application significantly improved all measured traits except stem fresh weight. Notable increases were observed in leaf length (44 cm), leaf area (726.5 cm²), chlorophyll content (48.8 SPAD units), and nitrogen concentration (3.25%). Moreover, the combined application of seaweed extract and salt stress substantially alleviated stress induced damage, leading to a 14% increase in leaf area and a 27% increase in potassium content compared to salt stressed plants. Seaweed based biostimulants therefore represent a promising and sustainable strategy to mitigate salt stress effects in tobacco cultivation.

Keywords Salinity · Seaweed extract · *Nicotiana tabacum* L. · Biostimulant · Nutrient elements

Introduction

Tobacco (*Nicotiana tabacum* L.) is an important industrial plant belonging to the Solanaceae family. Due to the nicotine and other alkaloid compounds found in its leaves, it is used in many sectors, primarily the cigarette industry (Shoji and Hashimoto 2011). Despite being an economically important agricultural product, tobacco farming has been declining year by year due to difficulties in production and the high average age of producers (Ekren and İlker 2017). For this reason, the tobacco sector attaches great importance to efforts to increase yield without compromising quality. There is research in many areas, such as variety cultivation techniques, fertilization, topping, and drying, which are among the leading yield-enhancing factors (Kurt and

Kınay 2021; Tepecik et al. 2024). Salt stress is another abiotic stress factor that limits production in tobacco farming. Salt stress is considered a significant limiting environmental factor on plant growth, physiological functions, and product quality. Increased soil salinity disrupts the osmotic pressure balance in the root zone, limiting water uptake, causing ion toxicity, and preventing the uptake of nutrients (K⁺, Ca²⁺, Mg²⁺), particularly due to the accumulation of Na⁺ and Cl⁻ ions (Shrivastava and Kumar 2015). This negatively affects leaf development, chlorophyll synthesis, and nicotine metabolism in tobacco plants, leading to reduced photosynthetic activity and yield losses (Dell'Aversana et al. 2021a). Salt stress also causes oxidative stress in tobacco, leading to the accumulation of reactive oxygen species (ROS), which causes serious physiological damage such as lipid peroxidation in cell membranes, protein denaturation, and impaired enzyme activity (Munns and Tester 2008). As a result, plant metabolism suffers energy loss and carbon assimilation decreases, leading to a reduction in leaf biomass. Wu et al. (2018) reported that the application of 100 mM NaCl in tobacco reduced leaf chlorophyll content by 30% and significantly decreased photosynthetic efficiency. Similarly, (Chen et al. 2020) indicated that salt stress suppresses nicotine

✉ İbrahim Halil Şındak
ibrahim.sindak@ege.edu.tr

¹ Faculty of Agriculture Department of Field Crop, Ege University, İzmir, Turkey

² Faculty of Agriculture, Department of Soil Science and Plant Nutrition, Ege University, İzmir, Turkey

synthesis in tobacco because ion imbalance and water deficiency inhibit the synthesis pathways of secondary metabolites. Consequently, salt stress causes significant losses in both quantity and quality in tobacco production; therefore, applications that increase salt tolerance (e.g., biostimulants or organic regulators such as) are of great importance in sustainable tobacco farming. Biostimulants are defined as naturally derived substances that promote plant growth in agricultural production, increase nutrient use efficiency, and enhance physiological resistance under abiotic stress conditions. Specifically, seaweed extracts, humic and fulvic acids, protein hydrolysates, microbial inoculants, and plant-derived organic compounds are included in the biostimulant groups (du Jardin 2015; Rouphael and Colla 2020). Research has shown that biostimulants promote root development in plants, thereby increasing water and nutrient uptake, enhancing photosynthetic activity, and strengthening antioxidant defense systems (Calvo and Kloepper 2014; Bulgari Franzoni et al. 2019). Furthermore, it has been reported that biostimulant applications reduce the need for fertilizer inputs by increasing the nitrogen and phosphorus use efficiency of plants, thereby contributing to environmental sustainability (Yakhin et al. 2017). Biostimulants are gaining importance in modern agriculture as a strategic component in stress management, yield increase, and environmentally friendly production systems (Khan et al. 2021; Benli and Çetinkaya 2023). The use of seaweed extracts has gained popularity due to their potential applications in organic and sustainable agriculture (Russo and Berlyn 1990). Algae are autotrophic and photosynthetic organisms that can live in a wide range of aquatic and semi-aquatic environments, such as oceans, rivers, freshwater lakes, streams, polar lakes, puddles, etc. (Üver Alçay et al. 2017). The algae sources used commercially on a large scale worldwide generally include four separate types of algae: Rhodophyta (red algae), Phaeophyta (brown algae), Chlorophyta (green algae), and Cyanophyta (blue-green algae) (Güner and Aysel 1996). The most common seaweed fertilizer materials on the market are mostly brown algae. This can be attributed to their higher natural phytohormone and micro- and macro-nutrient content compared to other algae species (Craigie 2011). Seaweed concentrates are effective biostimulants in many products, including vegetables, trees, flowering plants, and cereal crops (Stirk et al. 2004). In this context, biostimulants, particularly seaweed extracts, are attracting attention as alternative applications offering sustainable solutions in the agricultural field (du Jardin 2015; Rouphael and Colla 2020). Extracts obtained from brown algae (such as *Ascophyllum nodosum* and *Ecklonia maxima*) are reported to be rich in phytohormones (auxin, cytokinin, gibberellin), amino acids, betaines, phenolic compounds, vitamins, and polysaccharides, and these compounds are reported to have growth-promoting effects

on plant metabolism (Craigie 2011; Shukla et al. 2019). Seaweed extracts promote strong root development, enabling plants to absorb more nutrients and water from the soil, accelerate chlorophyll formation in plants, thereby increasing green biomass, and enhance plants' resistance to diseases, pests, and environmental stresses. They increase yield, improve quality, and enhance market value by ensuring the balanced and long-term uptake of macro and micro nutrients from the soil (Blunden et al. 1992; Hong et al. 2007). Seaweed extracts have protective effects against salt stress in plants. *Ascophyllum nodosum*-based applications have been shown to stabilize ion homeostasis by reducing Na^+ accumulation and improve water uptake by promoting the production of osmoprotectants such as proline and betaine (Dell'Aversana et al. 2021b). Furthermore, these extracts activate antioxidant defense systems (SOD, CAT, POD), providing protection against reactive oxygen species that damage cell membranes (Ali et al. 2021; Raja and Vidya 2023). Plant nutrient uptake is significantly impaired, especially under the influence of salt stress. Excessive accumulation of Na^+ inhibits the transport of macroelements such as K^+ , Ca^{2+} , and Mg^{2+} , while limiting the accumulation of microelements such as iron (Fe), zinc (Zn), and manganese (Mn) in tissues (Rengasamy 2010). Seaweed applications have been reported to facilitate element uptake by increasing root permeability and improving nutrient use efficiency (Deolu-Ajayi et al. 2022; Hernández Herrera et al. 2022). In terms of yield components, significant increases in morphological factors such as plant height, number of leaves, leaf width-to-length ratio, fresh and dry leaf yield have been reported in plants treated with seaweed extracts (Blunden and Wildgoose 1977; Khan et al. 2009). Furthermore, a synergistic effect has been observed in systems where seaweed and salt combinations were applied; thus, the negative effects of salt stress were reduced, resulting in net improvements in growth processes (Bhattacharyya et al. 2015; Rouphael et al. 2018). Although the effect of biostimulant applications on physiological parameters against salt stress in *N. tabacum* has been addressed in limited studies, the positive results obtained in similar model plants may also be valid for this plant. The effects of salt stress on *N. tabacum*, such as root growth, ion homeostasis, antioxidant defense, and nutrient uptake, have been studied in detail; evidence has been presented that these effects can be mitigated through biostimulation.

The objective of this study is to investigate the effects of salt stress, a significant limiting factor in tobacco farming, on yield, yield components (plant height, number of leaves, leaf size, dry matter), and plant nutrient uptake in tobacco plants through the application of seaweed. This study is original in that it investigates the effects of seaweed applications on Virginia type tobacco, a topic that has been addressed only to a limited extent in the literature,

particularly under salt stress conditions. Given that most existing studies primarily focus on Burley-type tobacco or non-stress conditions, this research represents one of the first comprehensive studies to systematically integrate morphological, physiological, and nutrient-related responses of Virginia tobacco under salt stress in relation to seaweed extract application. The findings highlight the coordinated role of these traits in stress adaptation and demonstrate the potential of seaweed treatments to alleviate the adverse effects of salinity, thereby providing novel and valuable contributions to both the scientific literature and sustainable tobacco production.

Materials and Methods

Study Sites and Experimental Setup

This study was conducted in controlled greenhouse conditions at Ege University Faculty of Agriculture between April and August 2024, using the K326 Virginia variety, in a randomized complete block design (RCBD) with three

replications. A germination test was performed on the seeds before sowing them in the pots. Since tobacco seeds are very small, they were germinated in a laboratory environment. Each tray filled with peat was sown with 2–3 seeds on December 20, 2023. The first seedlings emerged on January 7, 2024. The tobacco seedlings grown in the trays were transplanted on February 21, 2024, with two seedlings per pot. After planting, the seedlings were irrigated. On March 5, 2024, thinning was performed so that only one plant remained in each pot. The soil used in the experiment was sieved with a 2 mm sieve and filled into pots with a soil volume of 5 kg. The physical and chemical properties of the potting soil are listed in Table 1.

Fertilization Procedures

All pots were transplanted with tobacco seedlings, and basic fertilization was applied as follows: 15 kg/ha N, 10 kg/ha P_2O_5 , and 10 kg/ha K_2O , using ammonium sulfate for nitrogen, diammonium phosphate (DAP) for phosphorus, and potassium sulfate (K_2SO_4). Initially, the field capacity of the pot soil was determined, and the pots were weighed pe-

Fig. 1 Applications performed in the study

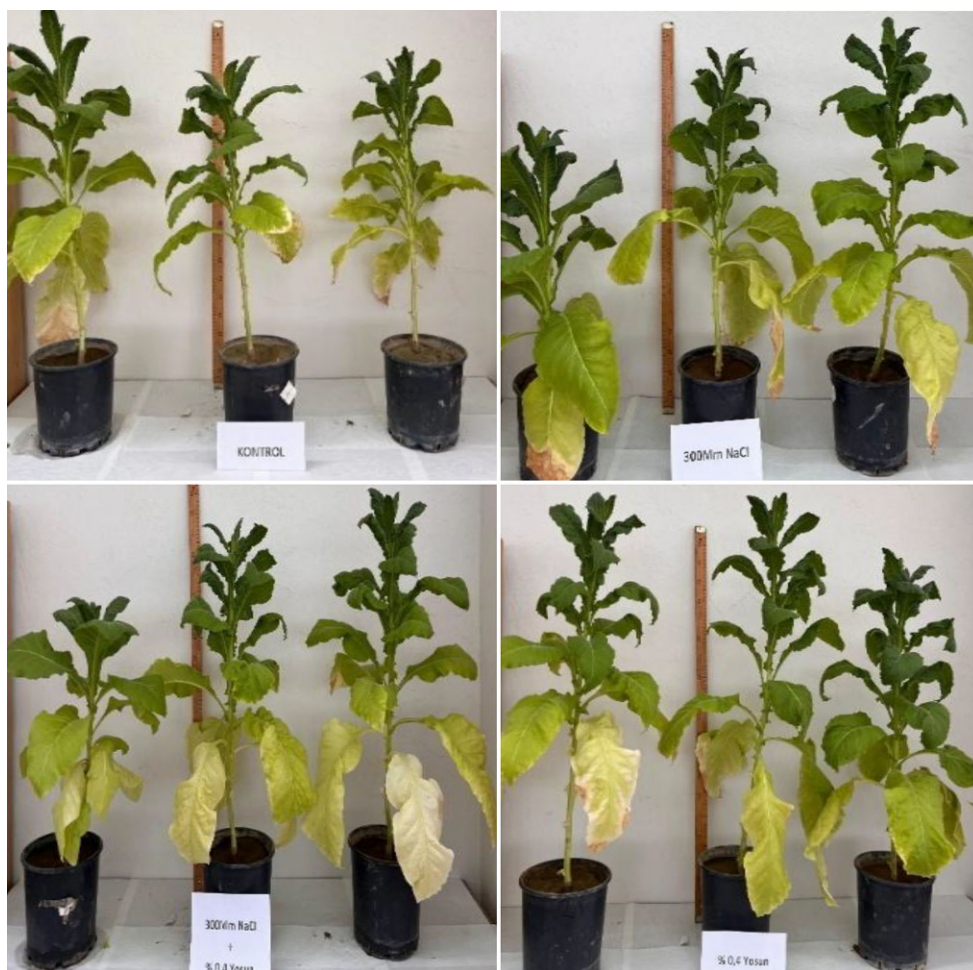


Table 1 Analysis results of potting soils

pH (1:2.5)	7.46	Available P (mg ^{kg} ⁻¹)	4.71
E.C (dS m ⁻¹)	0.21	Available K (mg ^{kg} ⁻¹)	148.40
Calcium (%)	6.12	Available Ca (mg ^{kg} ⁻¹)	2413.10
Sand (%)	68.96		
Silt (%)	18.00	Available Mg (mg ^{kg} ⁻¹)	143.70
		Available Na (mg ^{kg} ⁻¹)	68.50
Clay (%)	13.04	Available Fe (mg ^{kg} ⁻¹)	3.85
Soil structure	Sandy loam	Available Zn (mg ^{kg} ⁻¹)	0.36
Organic matter (%)	1.56	Available Mn (mg ^{kg} ⁻¹)	4.71
Total N (%)	0.072	Available Cu (mg ^{kg} ⁻¹)	0.40

riodically and irrigated with irrigation water to compensate for the decrease in moisture content (Karagöz et al. 2018). The first seaweed application was made immediately after transplanting healthy single plants into pots on the 20th day, and the second application was made on the 40th day by foliar application. In the control application, only pure water was applied to the leaves, and the seaweed extracts were applied to the leaves by thoroughly wetting the plants in each pot with 0.5l of water.

Experimental Applications

In the study, applications were made as Control (pure water), 0.4% Seaweed (SW), 300mM NaCl (S), and 300mM NaCl+0.4% Seaweed (S+SW) (Fig. 1). The analysis content of the seaweed used in the study is presented in Table 2. The necessary agronomic measurements were performed on tobacco plants that had reached harvest maturity. Harvesting was carried out on August 5, 2024, by manually breaking the leaves of the plants.

Character or Properties Examined in the Study

Plant height (cm): The length from the point where the plant emerges from the soil to its tip was measured using a ruler (Khan et al. 2009). **Number of leaves (number/plant):** The total number of leaves per plant in each pot was counted (Anonymous 2006). **Leaf width (cm):** The length of the widest part of the leaf was measured using a ruler. **Leaf length (cm):** The length between the base and tip of the leaf (cm) was determined. **Leaf area (cm²):** It was obtained using the formula: leaf width×leaf length×0.75. **Root length (cm):** The length from where the root first

emerges to its tip was measured using a ruler **Leaf fresh weight (g):** The leaves of the plants in each pot were separated from the stems and weighed on a scale. **Leaf dry weight (g):** After determining the fresh weight, the leaves were dried at 65–70 °C for 48 h and then weighed on a balance to determine the weight in grams (Ekren et al. 2021). **Root fresh weight (g):** The roots of each pot of plant were separated from the soil and then weighed on a balance to obtain measurements. **Root dry weight (g):** After determining the fresh weight, it was dried at 65–70 °C for 48 h and then weighed on a scale to determine the weight in grams. **Stem fresh weight (g):** The plant stem, separated from its leaves, was weighed on a scale and determined in grams. **Stem dry weight (g):** After determining the fresh weight, it was dried at 65–70 °C for 48 h and then weighed on a scale and determined in grams. **Drying process:** Drying was performed in an oven under controlled conditions according to the flue curing method (Abubakar et al. 2000). The dry weights of the dried tobacco leaves were measured after oven drying and ground for analysis. **Macroelement measurements: Total alkaloid nicotine ratio (%)** according to the method determined by (Lott et al. 1956; Baur and Ensminger 1977; Plank 1992; Hanlon 1992; Jones 2001; Kacar 1972; Anonymous 1986): According to the method specified by (Anonymous 1969), **crude ash ratio (%)**: According to the method developed by (Nelson 1960) and **chlorophyll content (SPAD):** According to the method developed by (Xu et al. 2000; Tepecik et al. 2024).

Statistical Analysis

Experiments were conducted in a randomized plot design with three replications. The analysis of variance (ANOVA) for the experimental data was performed using JMP (version 8.0) software, and significant differences among means were determined using the LSD test at the 5% significance level.

Table 2 Content of seaweed used in the study

Organic Matter	10%
Alginic Acid	0.80
Water-Soluble Potassium Oxide (K ₂ O)	4
Maximum EC	8.2 dS/m
pH Range	7.7–9.7

Table 3 Parameters related to the root and stem

Treatments	Root fresh weight (g)	Root dry weight (g)	Root length (cm)	Stem fresh weight (g)	Stem dry weight (g)
<i>Control</i>	11.46b	2.15b	16.03ab	82.49b	9.55b
<i>S</i>	7.20d	1.21d	15.33b	78.12b	7.03c
<i>SW</i>	13.61a	2.65a	17.50a	84.61b	10.65a
<i>SW + S</i>	9.42c	1.56c	17.07a	94.58a	8.76b
<i>Mean</i>	10.42	1.89	16.48	84.95	8.99
<i>F ratio</i>	79.2**	125.2**	4.27*	8.02**	33.68**
<i>LSD</i>	0.989	0.184	1.541	7.981	0.851

*, **, significant at 0.05 and 0.01, respectively; Means followed by the same letter are not significantly different

Results

Results Related to Roots and Stems

According to the data in the Table 3, different applications create statistically significant differences in plant growth parameters. When examining the overall averages, root fresh weight (RFW) was determined to be 10.42 g, root dry weight (RDW) 1.89 g, root length (RH) 16.48 cm, stem fresh weight (SFW) 84.95 g, and stem dry weight (SDW) 8.99 g. The highest RFW value was obtained with seaweed (SW) application at 13.61 g, while the lowest was obtained with salt (S) application at 7.20 g. Under salt stress, seaweed application (SW+S) showed a significant increase compared to salt application alone, with a value of 9.42 g. Similarly, the highest RDW value was observed in the seaweed application (2.65 g), while the lowest value was observed in the salt application (1.21 g). The SW+S application provided an improvement of approximately 29% in this parameter (1.56 g) compared to salt stress alone. The highest values for root length were observed in the SW (17.5 cm) and SW+S (17.07 cm) treatments, while the S treatment yielded the lowest result at 15.33 cm. This indicates that seaweed supports root development under stress conditions. The highest stem fresh weight (SFW) value was 94.58 g in the SW+S treatment, while the lowest value was 78.12 g in the S treatment. Furthermore, in terms of stem dry weight (SDW), the highest value was recorded in the SW application at 10.65 g, while the lowest value was recorded in the S application at 7.03 g. The SW+S application significantly reduced the negative effects of salt stress and increased dry matter accumulation at 8.76 g. Overall, it was determined that the salt (S) application yielded the lowest values for all parameters, whereas the seaweed application (SW and SW+S) mitigated the effects of stress and supported plant growth. These findings indicate that seaweed application has a protective effect on plant physiology and promotes growth under salt stress.

Table 4 Plant height, chlorophyll, and chemical content

Treatments	Plant height (cm)	SPAD	Nicotine (%)	Ash (%)
<i>Control</i>	71.00b	40.96b	1.56c	17.17c
<i>S</i>	68.00b	35.88c	1.51c	16.33c
<i>SW</i>	77.67a	48.80a	2.13a	21.00a
<i>SW + S</i>	67.67b	38.27b	1.74b	19.33b
<i>Mean</i>	71.08	40.98	1.74	18.46
<i>F ratio</i>	7.9**	22.2**	30.92**	19.5**
<i>LSD</i>	5.359	3.85	0.161	1.541

*, **, significant at 0.05 and 0.01, respectively; Means followed by the same letter are not significantly different

Results Related to Plant Height, Chlorophyll, and Chemical Content

According to the data in the Table 4, different applications have created statistically significant differences in plant physiological characteristics. In the study, the S application was applied as salt stress, and the SW application was applied as seaweed extract. The parameters evaluated were PH (plant height), SPAD (chlorophyll content), NIC (nicotine content), and ASH (ash content). When the general averages were examined, plant height was determined to be 71.08 cm, SPAD value 40.98, nicotine content 1.74, and ash content 18.46. The highest plant height value was 77.67 cm in the seaweed (SW) application, while the lowest value was 68.00 cm in the salt stress (S) application. Although the seaweed application under salt stress (SW+S) had a value close to that of the salt application at 67.67 cm, it was significantly lower than that of the SW group where seaweed was applied alone. This indicates that salt stress has an inhibitory effect on growth, but seaweed has a stimulating effect on growth outside the stress environment. When examining the SPAD value, the highest chlorophyll content was found in the SW application at 48.80, while the lowest value was found in salt stress (S) at 35.88. The SW+S application provided a partial increase of 38.27 compared to the salt application. This result indicates that the seaweed application reduces chlorophyll degradation by protecting photosynthetic pigments. In terms of nicotine con-

tent (NIC), the highest value was 2.13 in the SW application, and the lowest value was 1.51 in the S application. The SW + S application showed an increase of approximately 15% compared to the salt application alone, with a value of 1.74. This indicates that seaweed extract supports the plant's defense mechanisms by promoting nicotine synthesis under stress conditions. In the ash content (ASH) parameter, the highest value was determined to be 21.00 in the SW application, and the lowest value was determined to be 16.33 in the S application. The SW + S application provided an increase of approximately 18% compared to salt stress with a value of 19.33. This increase indicates that the seaweed application partially regulated the mineral imbalances caused by salt stress. Overall, the salt (S) application yielded the lowest values in all parameters, while the seaweed (SW) application provided the highest values for growth, chlorophyll accumulation, nicotine synthesis, and mineral content. The SW + S combination partially reduced the negative effects of salt stress and provided a significant improvement in physiological parameters. These findings indicate that seaweed extract has a biostimulant effect that supports plant growth under salt stress, preserves chlorophyll content, and increases the synthesis of nicotine, which is a defense metabolite.

Results Related to Fresh and Dried Leaf

According to the data in the Table 5, different applications have been found to cause significant differences in plant morphological and physiological parameters. The parameters evaluated are, respectively, LW (leaf width), LH (leaf length), LA (leaf area), NL (number of leaves), LFW (fresh leaf weight), and LDW (dry leaf weight). When the general averages were examined, leaf width was determined to be 20.55 cm, leaf length 39.75 cm, leaf area 618.7 cm², number of leaves 24.25, fresh leaf weight 683.7 g, and dry leaf weight 14.74 g. No statistically significant difference was found between treatments in terms of leaf width (LW) (LSD: ns), with values ranging from 19.4 to 22 cm. However, the highest leaf width was 22 cm in the seaweed (SW)

treatment, and the lowest value was 19.4 cm in the salt stress (S) treatment. This indicates that the seaweed application slightly promotes leaf development. In terms of leaf length (LH), the highest value was 44 cm in the seaweed (SW) application, while the lowest value was 35.5 cm in salt stress (S). Under salt stress, the seaweed application (SW + S) showed a significant increase of 40.4 cm compared to the salt application alone. This result indicates that seaweed has a supportive effect on leaf growth despite salt stress. The highest value for the leaf area (LA) parameter was 726.5 cm² in the SW application, while the lowest value was 532.3 cm² in the S application. The SW + S application provided an increase of approximately 14% compared to salt stress, with a value of 608.4 cm². Although there was no statistically significant difference between treatments in terms of leaf number (NL) (LSD: ns), the highest value was observed in the SW treatment at 25.33, and the lowest value was observed in the S treatment at 22.33. While salt stress limited the number of leaves, the seaweed application positively affected this parameter. In terms of leaf fresh weight (LFW), the highest value was obtained in the SW application with 1121.4 g, and the lowest value was obtained in the S application with 248.3 g. The SW + S application provided a leaf fresh weight of 832.4 g, which is approximately three times higher than that of the salt application alone. This finding shows that seaweed significantly reduces the negative effects of salt stress and increases leaf biomass. In terms of leaf dry weight (LDW), the highest value was 15.53 g in the SW + S application, while the lowest value was 13.19 g in the S application. Both the SW and SW + S applications showed high dry matter accumulation, similar to the control group. This indicates that seaweed application has a stimulating effect on dry matter accumulation in leaf tissue even under stress conditions. Overall, the salt (S) application yielded low values for all parameters, while the seaweed (SW) application provided the highest results in terms of both leaf morphology and biomass. The SW + S combination significantly reduced the negative effects of salt stress and provided noticeable improvements, particularly in leaf length, area, and fresh weight. These results

Table 5 Fresh and dried leaf characteristics

Treatments	Leaf width (cm)	Leaf height (cm)	Leaf area (cm ²)	Number of leaves (number/plant)	Leaf fresh weight (g)	Leaf dry weight (g)
Control	20.8	39.07bc	607.4b	25.00	532.8c	14.86a
S	19.4	35.50c	532.3c	22.33	248.3d	13.19b
SW	22.0	44.00a	726.5a	25.33	1121.4a	15.38a
SW + S	20.0	40.40ab	608.4b	24.33	832.4b	15.53a
Mean	20.55	39.75	618.7	24.25	683.7	14.74
F ratio	3.58 ^{ns}	9.31 ^{**}	19.94 ^{**}	2.7 ^{ns}	233.1 ^{**}	6.01 [*]
LSD	1.91	3.72	58.44	2.65	80.27	1.403

*, **, significant at 0.05 and 0.01, respectively; Means followed by the same letter are not significantly different

clearly demonstrate that seaweed extract has a biostimulant effect on plants, enhancing leaf development, biomass formation, and physiological resilience against salt stress.

Results Related to Macro Element Content

When the overall averages are examined, nitrogen was determined to be 2.56%, phosphorus 0.43%, potassium 2.69%, calcium 3.50%, and magnesium 0.47%. The highest nitrogen (N) content was 3.25% in the seaweed (SW) application, while the lowest was 2.17% in the salt stress (S) application. The SW + S application showed an increase of approximately 12% compared to salt stress, with a value of 2.44%. This indicates that seaweed reduces the negative effects of salt stress by supporting nitrogen uptake. A similar trend was observed in phosphorus (P) content. The highest value was 0.54% in the SW application, while the lowest value was 0.37% in the control group. Under salt stress, the seaweed application (SW + S) showed an increase to 0.42% compared to the salt application alone (0.39%). In terms of potassium (K) content, the highest value was 3.13% in the SW application, while the lowest value was 2.24% in the S application. The SW + S application provided an increase of approximately 27% compared to salt stress, with a value of 2.84%. This increase indicates that seaweed regulates ion balance, thereby increasing potassium accumulation. In terms of calcium (Ca) content, the highest value was obtained in the SW + S application at 3.83%, while the lowest value was observed in the control group at 3.13%. Salt stress (3.58%) also increased calcium content compared to the control group, indicating that plants tend to increase calcium accumulation to strengthen cell walls under stress

Table 6 Macro element content

Treatments	N (%)	P (%)	K (%)	Ca (%)	Mg (%)
Control	2.38bc	0.37c	2.56c	3.13c	0.49b
S	2.17c	0.39bc	2.24d	3.58ab	0.39c
SW	3.25a	0.54a	3.13a	3.47b	0.54a
SW + S	2.44b	0.42b	2.84b	3.83a	0.46b
Mean	2.56	0.43	2.69	3.50	0.47
F ratio	40.16**	36.77**	23.67**	8.21**	21.08**
LSD	0.23	0.039	0.253	0.33	0.043

** Means followed by the same letter are not significantly different ($p < 0.01$)

conditions. However, the SW + S application achieving the highest calcium ratio proves that seaweed plays a supportive role in this process. The highest magnesium (Mg) content was found in the seaweed (SW) application at 0.54%, while the lowest value was detected in salt stress (S) at 0.39%. The SW + S application showed a significant improvement over salt stress alone, with a value of 0.46%. This increase indicates that seaweed application facilitates magnesium uptake, supporting chlorophyll synthesis and photosynthetic activity. Overall, salt stress (S) caused a decrease in all nutrient elements, whereas seaweed (SW) application provided a significant increase in the content of all macro nutrients (N, P, K, Ca, Mg). The SW + S combination significantly improved the nutrient imbalances caused by salt stress, creating levels close to or higher than the control group (Table 6). These results clearly demonstrate that seaweed extract exhibits a biostimulant effect in plants under salt stress, increasing nutrient uptake, regulating ion balance, and enhancing physiological resilience.

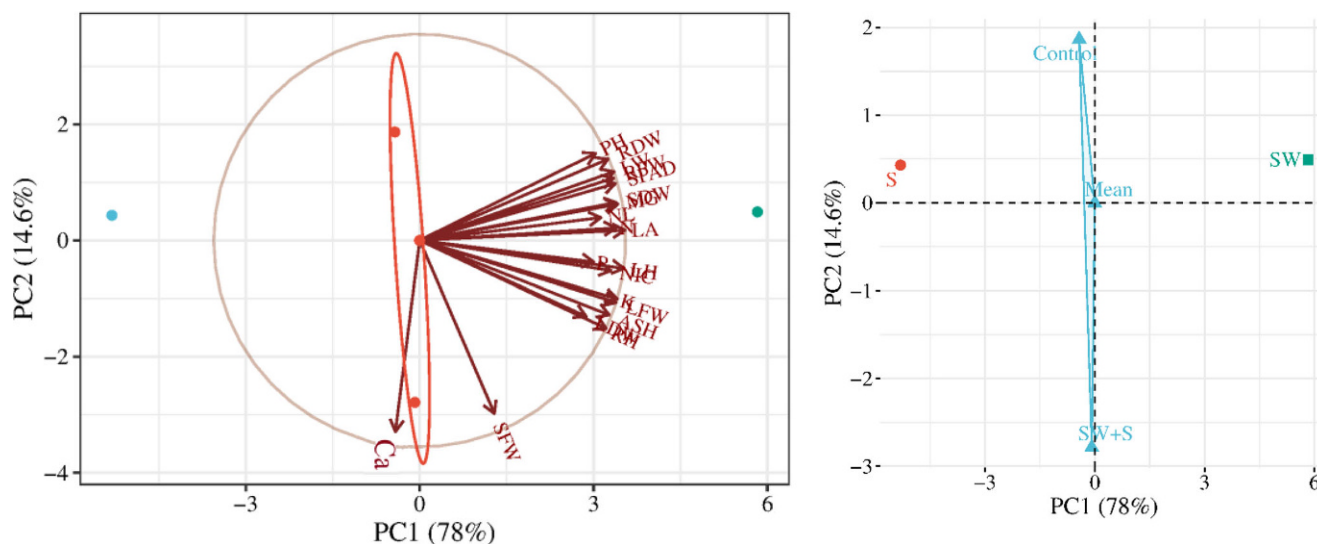


Fig. 2 PCA analysis (RFDW (root fresh weight), RDW (root dry weight), RL (root length), SFDW (shoot fresh weight), SDW (shoot dry weight), SPAD (Soil Plant Analysis Development), LW (leaf width), LH (leaf height), LA (leaf area), NIC (nicotine content), N (nitrogen), P (phosphorus), K (potassium), Ca (calcium), Mg (magnesium))

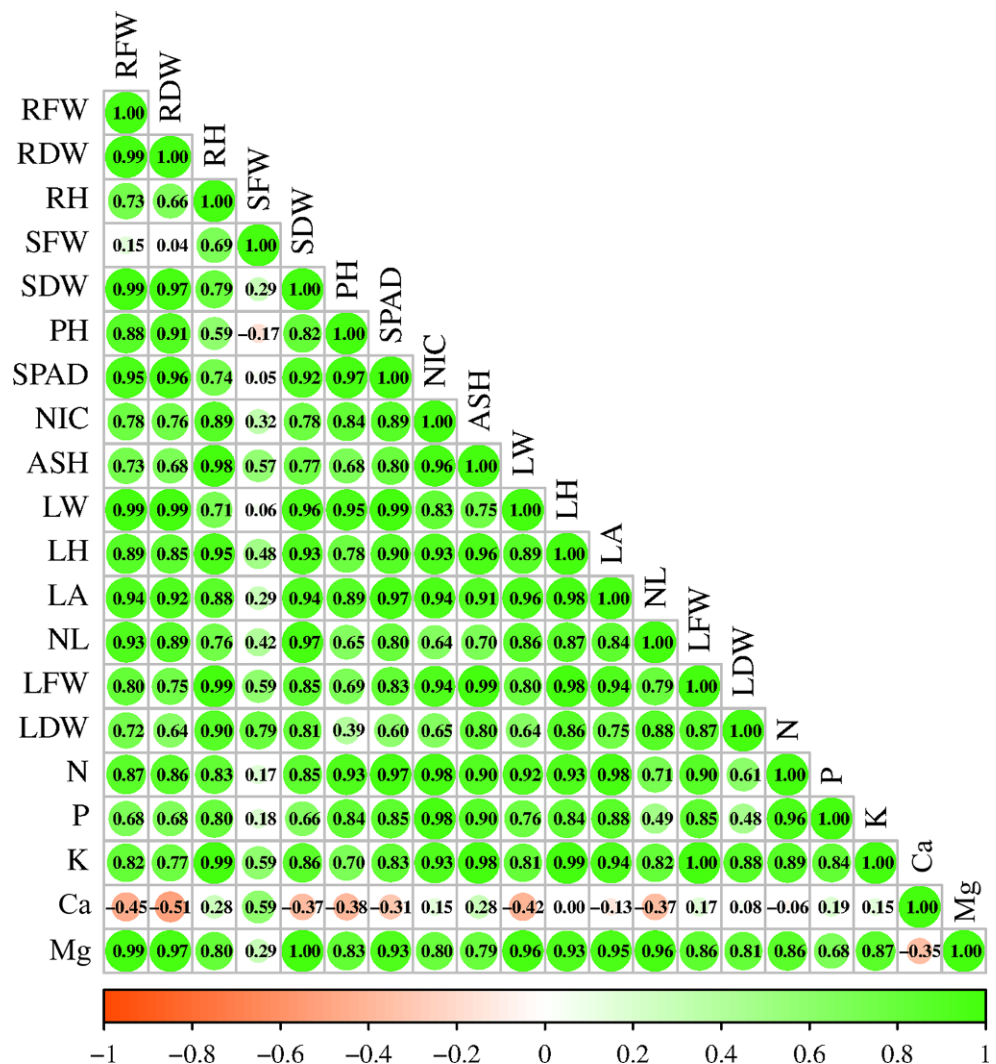
PCA Analysis

The PC1 axis (78%) explains the majority of the variation. This means that the largest part of the difference between seaweed and salt stress plant responses is represented on this axis. The application of SW (seaweed) showed a strong separation on the right side of the graph in the positive PC1 direction. This indicates that the seaweed application had positive effects on the parameters examined (e.g., LA, LFW, LDW, SPAD, PH) and that these parameters had high values. The salt stress (S) treatment, on the other hand, is located in the negative PC1 region on the left side. This indicates that salt stress generally has a negative effect on the parameters and causes a decrease, particularly in growth, leaf development, and physiological values. The control group exhibited a neutral position, located around the mean point. The SW + S (seaweed under salt stress) application was positioned in a downward-sloping region close to the mean point (Fig. 2). This indicates that seaweed showed a partial ameliorative effect under salt stress conditions.

Correlation Analysis

The results of the correlation analysis indicate that there are generally strong and significant positive relationships between the morphological, physiological, and chemical parameters examined in the tobacco plant. The correlation coefficient between most parameters is $r > 0.80$, which indicates that the growth and physiological processes in the plant are highly coordinated. Very strong correlations ($r = 0.88–0.99$) were found between RFW (root fresh weight), RDW (root dry weight), SDW (stem dry weight), and PH (plant height). This indicates that root and stem development progressed in parallel and that biomass production was directly related to plant height. Similarly, high positive correlations ($r = 0.86–0.98$) were observed between parameters related to leaf morphology, namely LW (leaf width), LH (leaf length), LA (leaf area), and NL (number of leaves). This indicates that leaf morphological components show a tendency to increase or decrease together and that leaves are complementary indicators of plant growth.

Fig. 3 Correlation analysis (RFW (root fresh weight), RDW (root dry weight), RL (root length), SFW (shoot fresh weight), SDW (shoot dry weight), SPAD (Soil Plant Analysis Development), LW (leaf width), LH (leaf height), LA (leaf area), NIC (nicotine content), N (nitrogen), P (phosphorus), K (potassium), Ca (calcium), Mg (magnesium))



LFW (leaf fresh weight) and LDW (leaf dry weight) were also found to be highly correlated with other growth parameters (especially LA, LH, PH) ($r=0.85\text{--}0.98$). This indicates that leaf development is directly linked to photosynthetic activity and biomass accumulation. SPAD (chlorophyll content) showed a high positive correlation with almost all growth parameters (PH, LA, LFW, RDW, etc.) ($r=0.92\text{--}0.97$). This indicates that leaf area and chlorophyll accumulation in plants follow a parallel course and that the amount of chlorophyll reflects the overall photosynthetic capacity. NIC (nicotine content) shows positive correlation ($r=0.76\text{--}0.89$) with parameters such as SPAD, PH, and LA. This indicates increased metabolic activity (particularly alkaloid synthesis) along with leaf physiology. The increase in leaf biomass and chlorophyll content may also contribute to nicotine biosynthesis. ASH (ash content) is also moderately to highly positively correlated with LA, PH, and SPAD ($r=0.68\text{--}0.77$). This indicates that ash content is related to mineral accumulation in tissues. High positive correlations ($r=0.84\text{--}0.96$) were determined between N, P, K and Mg elements. Ca (calcium) showed negative correlations with most other parameters ($r=-0.35$ to -0.51). This indicates that calcium accumulation generally moves in the opposite direction to other growth and physiological processes (Fig. 3).

Discussion

Leaf Morphology and Physiology

This study on leaf morphology and physiology demonstrates that different applications create significant differences in plant parameters. When parameters such as leaf width (LW), leaf length (LH), leaf area (LA), number of leaves (NL), leaf fresh weight (LFW), and leaf dry weight (LDW) were examined, the positive effects of seaweed (SW) application were clearly evident. For example, the SW application increased leaf width up to 22 cm and raised leaf fresh weight to 1121.4 g. Ali et al. (2021) reported that seaweed extracts enhanced root development, chlorophyll accumulation, and biomass production in horticultural crops under abiotic stress conditions. Similarly, Kumar et al. (2024) emphasized that seaweed based biostimulants improve leaf growth and physiological resilience under salinity stress. These findings are consistent with the improved leaf morphology and biomass accumulation observed in tobacco plants in the present study. The salt stress (S) treatment, on the other hand, caused decreases in all parameters. Leaf length decreased to 35.5 cm, and leaf area decreased to 532.3 cm². Dell'Aversana et al. (2021a) reported that salinity stress reduced leaf expansion, nitrogen metabolism, and biomass accumulation in tomato plants, which is consis-

tent with the reduced leaf area and leaf length observed in tobacco in the present study. However, the SW + S combination reduced the negative effects of salt stress and increased leaf length to 40.4 cm and leaf area to 608.4 cm². Di Stasio et al. (2020) demonstrated that seaweed extract applications improved yield and osmotic adjustment in salt stressed tomato plants, whereas Ma et al. (2025) reported enhanced saline alkaline stress tolerance and biomass production in maize following seaweed biostimulant supplementation. Overall, seaweed applications positively affect plant growth and development and reduce the negative effects of salt stress. These findings indicate that seaweed extracts possess biostimulant properties and can be used as a potential tool for managing stress conditions in agriculture (Shahzad et al. 2023; Kumar et al. 2024).

Agronomic and Chemical Properties

The results obtained in this study clearly demonstrate that salt stress (S) has an inhibitory effect on growth, chlorophyll content, nicotine synthesis, and mineral accumulation in tobacco plants. The significant reduction in plant height under salt stress indicates that salt restricts water uptake through osmotic pressure changes and inhibits cell expansion. Shrivastava and Kumar (2015) reviewed salinity induced reductions in plant height, biomass accumulation, and leaf development across several crop species under saline conditions. These findings are consistent with the low plant height value of 68 cm in our study. The significant increases in plant height, chlorophyll content, and ash ratio obtained with seaweed extract (SW) application demonstrate the growth-promoting effect of this biostimulant. Benli and Çetinkaya (2023) noted that seaweed extracts derived from *Ascophyllum nodosum* contain hormone-like compounds (cytokinin, auxin, gibberellin) and that these compounds increase cell division, root development, and photosynthetic activity. Kumar et al. (2022) reported that seaweed extracts maintained chlorophyll stability and enhanced antioxidant defense systems in salt stressed plants. This information is consistent with the highest SPAD value of 48.8 observed in our study under SW application. The significant reduction in chlorophyll content (35.88) due to salt stress can be explained by the breakdown of pigments associated with increased reactive oxygen species (ROS) under stress conditions. Bharath Raja and Vidya (2023) reported that seaweed extracts maintain chlorophyll stability by reducing ROS accumulation, thereby sustaining photosynthetic capacity. This is consistent with the partial improvement in chlorophyll content observed in our study with the SW + S combination compared to salt stress. In terms of nicotine content (NIC), the high value obtained in the group where the seaweed extract was applied alone (2.13) indicates an increase in the plant's secondary metabolic activities. Phenolic compounds

and oligosaccharides contained in seaweeds can function as signaling molecules that activate plant defense mechanisms (Bhattacharyya et al. 2015). Similarly, numerous studies have reported that increased nicotine accumulation in tobacco plants under stress conditions is considered a defense response (Shoji and Hashimoto 2011). Therefore, the observed increase in nicotine synthesis with seaweed application can be interpreted as a response to biostimulation enhancing stress tolerance. The high ash content value (21.0) obtained with SW application indicates the mineral balance-regulating effect of seaweed. Khan et al. (2021) stated that seaweed extract applications increased the accumulation of essential nutrient elements such as Ca, K, Mg, and Fe in plant tissues. This is parallel to the 18% increase in ash content achieved by the SW + S application in our study compared to salt stress.

Leaf Characteristics

The data obtained in this study show that salt stress (S) has an inhibitory effect on leaf morphological characteristics and physiological mass parameters in tobacco plants, while seaweed extract (SW) application has an ameliorative effect. The significant increases in leaf width, length, area, number, and especially fresh and dry weight values following seaweed application indicate that this biostimulant promotes plant growth and development processes. Shrivastava and Kumar (2015) stated that salt stress reduces water potential in plant tissues, decreasing leaf width and surface area. This explains the low leaf length (35.5 cm) and leaf area (532.3 cm²) in the S application in our study. Seaweed application (SW) provided the highest values for all parameters and created significant improvements compared to the control group, especially in morphological indicators such as leaf length (44 cm), leaf area (726.5 cm²), and fresh leaf weight (1121.4 g). This result is consistent with studies reporting that plant hormones (cytokinin, auxin, gibberellin) and organic compounds contained in seaweed extracts support leaf tissue development by increasing cell expansion, photosynthesis rate, and carbon assimilation (Benli and Çetinkaya 2023; Bhattacharyya et al. 2015).

Seaweed application (SW + S) under salt stress provided significant increases in leaf length, area, and fresh weight compared to salt application alone. This suggests that seaweed extracts increase water retention capacity by regulating osmotic imbalances caused by salt stress. Bharath Raja and Vidya (2023) emphasized that seaweed-based biostimulants maintain ion balance under stress conditions and sustain plant growth by improving leaf water potential. Similarly, Kumar et al. (2022) reported that seaweed extracts support leaf growth by maintaining chlorophyll stability and photosynthetic efficiency in plants under salt stress. This literature explains the physiological basis for the in-

crease in leaf area (14%) and biomass (832.4 g) observed in our study with the SW + S application. The high values observed in both SW and SW + S applications in terms of leaf dry weight (LDW) indicate that seaweed extract promotes carbon fixation and organic matter accumulation. Khan et al. (2021) stated that seaweed applications increase dry matter and total biomass accumulation in plant tissues by stimulating carbon metabolism. These results indicate that the high LDW value of 15.53 g in our study can be explained biochemically by the effect of seaweed. Although there was no statistically significant difference in leaf number, the highest average (25.33) obtained in the SW application suggests that seaweed extract indirectly promotes leaf formation. This finding is consistent with the results reported by Benli and Çetinkaya (2023), who stated that seaweed extracts with high salicylic acid and phenolic compound content support lateral tissue development.

Changes in Macro Element Content

The results obtained from the study reveal that salt stress (S) significantly limits the uptake of macro nutrients in tobacco plants, whereas the application of seaweed extract (SW) has a nutrient uptake-enhancing and ion balance-regulating effect. Significant increases were obtained in nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), and magnesium (Mg) contents with seaweed application. Shrivastava and Kumar (2015) reported that salt stress disrupts osmotic pressure balance, reducing root membrane permeability, which in turn limits nitrogen and potassium uptake in particular. This explains the observation of the lowest N (2.17%) and K (2.24%) values in the S application in our study. Seaweed extract application (SW) achieved the highest values for all nutrient elements. In particular, the increase in nitrogen content to 3.25% can be attributed to the supportive effect of these extracts on microbial activity and ammonium-nitrate conversion in the root zone. Khan et al. (2021) stated that seaweed applications accelerate the nitrogen cycle by increasing microbial density in the rhizosphere and increase the amount of nitrogen available to plants. Similarly, Bhattacharyya et al. (2015) emphasized that amino acids, polyphenols, and hormone-like compounds contained in seaweed extracts stimulate nitrogen metabolism, promoting protein synthesis. These explanations support the finding in our study that SW application provided the highest N content. The increase in phosphorus (P) content observed with SW application (0.54%) can be attributed to the seaweed's effect of increasing root surface activity and phosphorus solubility. Bharath and Vidya (2023) reported that seaweed-based biostimulants facilitate the transport of phosphate ions by stimulating root development. Furthermore, Benli and Çetinkaya (2023) stated that seaweed extracts increase phosphorus uptake in plants

and that this effect is related to the activation of carrier proteins in the root cell membrane. The 27% increase observed in potassium (K) content demonstrates the ion balance-regulating effect of seaweed extract. Kumar et al. (2022) reported that seaweed applications increase potassium retention by lowering the Na^+/K^+ ratio, thereby maintaining cellular osmotic balance. This finding parallels the significant increase in the potassium ratio (2.84%) in the SW + S application compared to salt stress in our study. The highest calcium (Ca) content was obtained in the SW + S application (3.83%). This indicates that seaweed extract supports cell wall stability by increasing calcium transport. Khan et al. (2021) emphasized that seaweed applications regulate cell membrane permeability and strengthen ion balance by stimulating Ca and Mg uptake. Furthermore, the partial increase in Ca observed under salt stress (3.58%) can be explained by the mechanism of plants accumulating calcium under stress conditions to increase structural resilience (Shrivastava and Kumar 2015). Furthermore, Weng et al. (2022) reported that calcium enhances stress tolerance by increasing cell wall and membrane stability, while Wan et al. (2013) reported that calcium accumulation improves resilience in plant tissues by increasing pectin and cell wall components. The increase in magnesium (Mg) content observed with SW application (0.54%) indicates that seaweed extracts support the activity of enzymes involved in chlorophyll synthesis. Benli and Çetinkaya (2023) reported that seaweed applications increase magnesium accumulation and enhance photosynthetic efficiency by regulating chlorophyll biosynthesis. This explanation is consistent with the high Mg contents found in the SW and SW + S applications in our study. Overall, while salt stress (S) created negative effects on all physiological parameters, seaweed extract (SW) application showed significant improving effects on growth, chlorophyll accumulation, defense metabolites, and mineral balance. Furthermore, the SW + S combination partially reduced the harmful effects of salt stress, leading to improvements in plant physiology. These results indicate that seaweed extracts can be used as biostimulants under salt stress and can support both growth and defense responses in metabolically sensitive plants such as tobacco.

Conclusion

In conclusion, the findings of this study demonstrate that seaweed extracts can serve as a sustainable biotechnological tool to enhance salt stress tolerance in plants. Moreover, this study provides the first clear evidence that seaweed applications significantly mitigate the adverse effects of salt stress in Virginia-type (K326 variety) tobacco, thereby addressing an important gap in the current literature. Future

research evaluating the effects of different seaweed species, application rates, and stress intensities will further clarify the agricultural potential of seaweed based biostimulants.

Author contributions SE and MT designed this study and conducted the experiments. IHS and HK collaborated on the statistical analyses and prepared the original draft. All co-authors contributed to the writing and editing of the final manuscript.

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Data Availability No datasets were generated or analysed during the current study.

Declarations

Competing interests The authors declare no competing interests.

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